

Suppression of the Black Phenotype in Females of the *P. glaucus* Group (Papilionidae)

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Abstract. Crosses between *Papilio g. glaucus* and *P. eurymedon* produced fertile offspring of both sexes, and backcrosses to *P. g. glaucus* revealed an autosomal suppressor in *P. eurymedon* which prevents expression of the black female phenotype of *P. g. glaucus*. Similar suppressors are demonstrated in *P. rutulus*, *P. multicaudatus* and *P. g. canadensis*.

Introduction

It is well known that in *Papilio glaucus* Linnaeus 1764, black females usually produce black daughters and yellow females yellow ones, irrespective of the provenance of the male. Occasional exceptions to this rule have been reported over many years and various explanations given (Clarke and Sheppard, 1959; Clarke et al., 1976). The present paper highlights the importance of autosomal genes which suppress, to a greater or less extent, the black female wing pattern. This can occur in the wild or be laboratory produced, and the phenomenon occurs in various species of the group.

In Section I we report a new example, bred by one of us (D.A.W.) in hybrids between black *glaucus* and *Papilio eurymedon* Lucas 1852.

Section II deals with further examples of suppression of black by *P. rutulus* Lucas 1852, *P. glaucus canadensis* Rothschild & Jordan 1906 and probably by *Papilio multicaudatus* Kirby 1884 (C.A.C.).

Section I: Suppression of Black in Hybrids Between *P. glaucus* and *P. eurymedon* (D.A.W.)

Papilio eurymedon (Fig. 1&2) is closely related to two other North American Swallowtails, *Papilio glaucus* (Fig. 11-13) and *Papilio rutulus* (Brower, 1959). Although laboratory crosses between *P. eurymedon* and *P. rutulus* have not been reported, Wagner (1978) described an almost certain male hybrid of these species from Idaho. In 1956 hybrids were

obtained between black and yellow female *glaucus* and male *P. eurymedon* (see Clarke and Sheppard, 1957) but only male insects were produced. In the present paper an account is given of female hybrids which were obtained (D.A.W.), and these are very informative as regards a gene suppressing the black of *glaucus*.

Materials and Methods

P. eurymedon were provided by Michael Collins from the vicinity of Nevada City, Nevada Co., California and Monitor Pass, Mono Co., California. They were collected as pupae from native food plants, *Ceanothus integerrimus* Hooker & Arnott (Rhamnaceae) and *Prunus virginiana*, var. *demissa* (Nuttall) (Rosaceae), in late summer 1984 and 1985 and eclosed in the laboratory in Blacksburg the following springs. *P. glaucus* were reared from local stock (Montgomery Co., Virginia) or from Wisconsin and Illinois stock provided by J. Mark Scriber. The latter originated from south of the principal zone of interaction of *P. g. glaucus* and *P. g. canadensis* in Wisconsin (Scriber et al. 1986 and see Section II). The insects were hand-paired, and the females laid eggs on *Prunus serotina* Ehrhart (a local foodplant of *P. glaucus*). Larvae were reared on this species, either in tight plastic boxes or on leafy stems kept turgid in Aquapics® in ventilated plastic canisters. Rearing was on natural mid-summer day length supplemented to 15 to 16 h by artificial light.

Samples of *P. glaucus* from Virginia and West Virginia and of *P. eurymedon* from northern California and western Oregon were used for morphological comparisons with the hybrids. *P. eurymedon* differs from *P. glaucus* most conspicuously in ground color, which is white or very pale yellow in the former but bright yellow in males and some yellow females of the latter. Some yellow females of *P. glaucus* are more orange-yellow. The black stripes and wing margins of *P. eurymedon* are broader than those of *P. glaucus*. As an index of the extent of the black pattern, the width of the under forewing black margin from its inner edge to the margin of the wing along vein Cu_1 was divided by the length of vein Cu_1 from the cell to the wing margin. The resulting ratio separates *P. glaucus* from *P. eurymedon*.

Results

Table 1 summarizes the successful crosses and Table 2 the unsuccessful ones. The F_1 hybrids (Broods 85.1 and 86.1, Figs. 3, 4, 15) are nearly intermediate between the parental species in the black pattern, in the larval thoracic eye spots (as in Clarke and Sheppard, 1957, Fig. 1) and in pupal proportions. As Clarke and Sheppard (1957) noted, the hybrid pupae do not show the green/brown dimorphism of *P. eurymedon*, all being brown as in *P. glaucus*. In fact the female pupa of brood 85.2 had some green markings, but they were in areas in which occasional *P. glaucus* pupae are green and not in the well-defined zones in which that color is found in green *P. eurymedon* pupae. In both sexes the ground color of the wings is nearly as yellow as that of *P. glaucus*. The submarginal spots on the upper and under sides of the hindwing of *P.*

Table 1. Successful matings between *Papilio glaucus* and *P. eurymedon*.

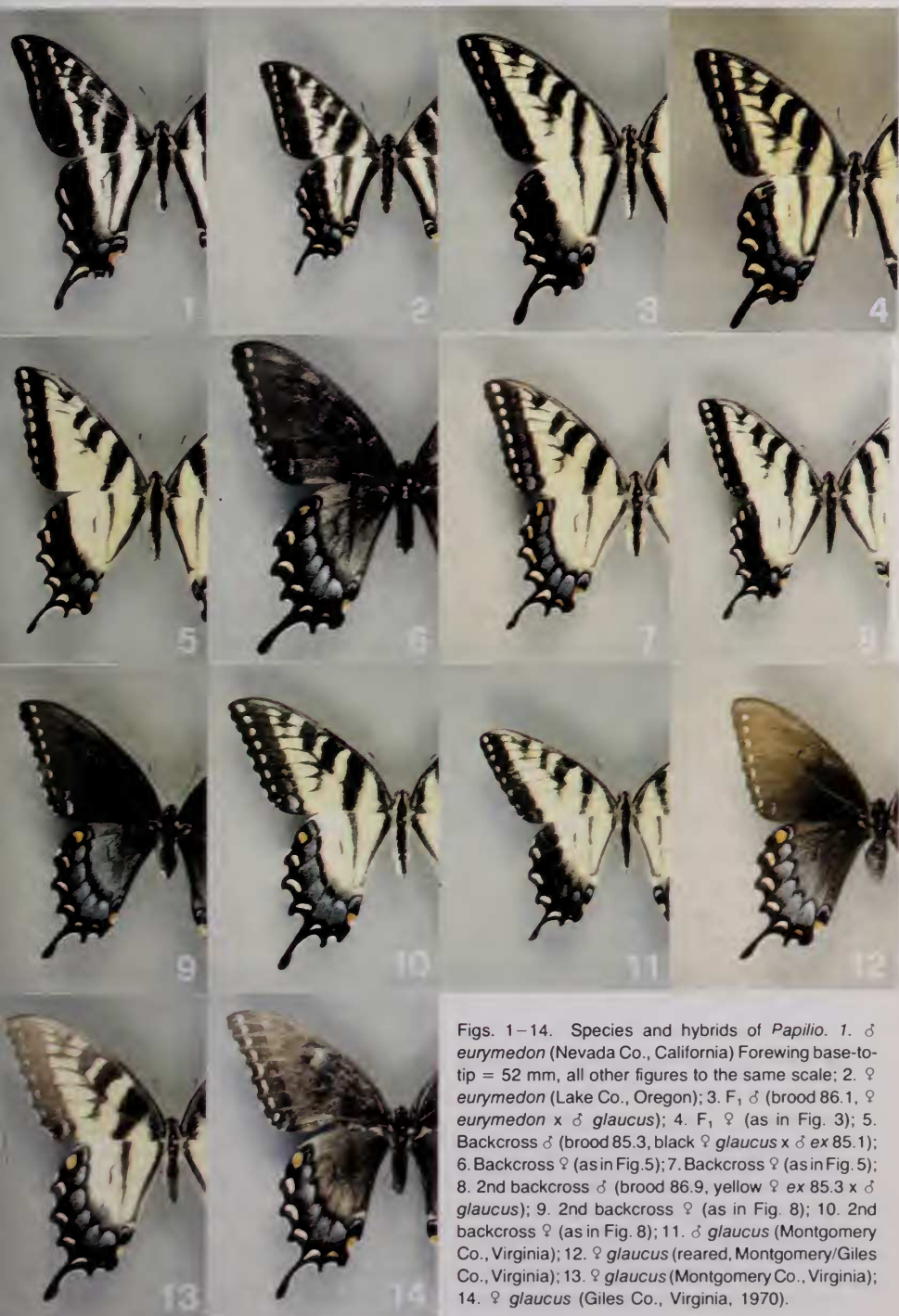
Mating No. and date	Mother	Source of Parents	Father	Eggs Laid	Eggs Devel.	Eggs Hatch.	Pupae	Eclosions
85.1 6 June 85	<i>eurymedon</i> (Nev. City, CA)	<i>glaucus</i> (WI)	<i>glaucus</i> (WI)	17	15	15	5 ♂♂ 2 ? sex	2 ♂♂ 3 ♂♂ died as pupae 2 ? sex lost
85.2 6 June 85	yellow <i>glaucus</i> (WI)	<i>eurymedon</i> (Nev. City, CA)	<i>eurymedon</i> (Nev. City, CA)	28	3	3	1 ♀ 1 ? sex	♀ pupa died Nov 86 Other pupa lost
86.1 25 May 86	<i>eurymedon</i> (Monitor Pass, CA)	<i>glaucus</i> (unknown)	<i>glaucus</i> (unknown)	31	30	27	13 ♀♀ 13 ♂♂	13 yellow hybrid-like ♀♀ 13 hybrid-like ♂♂
85.3 3 Aug 85	black <i>glaucus</i> (WI x IL)	<i>glaucus</i>	F ₁ ex 85.1	66	22	21	10 ♀♀ 9 ♂♂	2 black ♀♀ both intermediate 2 yellow ♀♀ 3 ♂♂ 6 ♀♀, 6 ♂♂ died as pupae
86.7 15 July 86	yellow <i>glaucus</i> (unknown)	<i>glaucus</i>	F ₁ 'G' ex 86.1	46	44	36	5 ♀♀ 11 ♂♂	4 yellow ♀♀ 9 ♂♂ 1 ♀, 2 ♂♂ died as pupae
86.12 17 July 86	yellow <i>glaucus</i> (unknown)	<i>glaucus</i>	F ₁ 'L' ex 86.1	11	3	3	2 ♀♀	1 yellow ♀ 1 ♀ died as pupa
86.8 15 July 86	F ₁ 'J' ex 86.1	<i>glaucus</i>	F ₁ 'H' ex 86.1	29	29	8	2 ♀♀	1 ♀ pupa alive, Mar. 88 1 ♀ died as pupa
86.9 16 July 86	yellow backcross ex 85.3	<i>glaucus</i> (unknown)	<i>glaucus</i> (unknown)	51	37	15	7 ♀♀ 7 ♂♂	1 yellow ♀, 6 black ♀♀ 5 ♂♂ 2 ♂♂ died as pupa
86.11 17 July 86	F ₁ 'O' ex 86.1	<i>glaucus</i>	F ₁ 'Q' ex 86.1	15	15	3	2 ♂♂	2 ♂♂

Table 2. Unsuccessful matings between *Papilio glaucus* and *P. eurymedon*.

Mating No. and date	Source of Parents Mother	Father	Remarks
86.3 28 May 86	yellow <i>glaucus</i> (unknown)	<i>eurymedon</i> (Nev. City, CA)	14 infertile eggs (no spermatophore)
86.4 31 May 86	<i>eurymedon</i> (Nev. City, CA)	<i>glaucus</i> (unknown)	41 infertile eggs
4 June 86	"	<i>glaucus</i> (unknown)	28 infertile eggs (1 tiny spermatophore)
86.5 14 July 86	yellow <i>glaucus</i> (unknown)	F ₁ 'A' ex 86.1	12 infertile eggs
19 July 86	"	F ₁ 'L' ex 86.1	unsuccessful pairing
19 July 86	"	F ₁ 'Q' ex 86.1	very long pairing (1 spermatophore?)
86.6 14 July 86	F ₁ 'B' ex 86.1	F ₁ 'D' ex 86.1	20 infertile eggs (1 spermatophore)
86.10 17 July 86	F ₁ 'N' ex 86.1	<i>glaucus</i> (unknown)	2 infertile eggs (very long pairing, no spermatophore)
86.13 29 July 86	F ₁ 'Y' ex 86.1	F ₁ 'P' ex 86.1	39 infertile eggs (1 spermatophore)
86.14 29 July 86	yellow <i>glaucus</i> (unknown)	F ₁ 'T' ex 86.1	23 infertile eggs (1 spermatophore)

glaucus are variable in size, shape and color but are usually rounder and oranger than those of *P. eurymedon*. The hybrids are also variable in these spots but are closer to *P. glaucus* in color and intermediate in size and shape. In all respects the male hybrids in broods 85.1 and 86.1 resemble those described by Clarke and Sheppard (1957) from the reciprocal species cross.

Brood 85-3, a backcross of a male F₁ from brood 85.1 to the black female form of *P. glaucus*, produced males (Fig. 5) and females of both forms: two black ones with a somewhat intermediate phenotype (Fig. 6), resembling occasional specimens taken in Virginia (Fig. 14), and two yellow ones (Fig. 7). One of the yellow females was backcrossed again, to a male *P. glaucus* (brood 86.9). All of the female pupae developed, and they produced six black and one yellow adults (Fig. 9 and 10; male in



Figs. 1-14. Species and hybrids of *Papilio*. 1. ♂ *eurymedon* (Nevada Co., California) Forewing base-to-tip = 52 mm, all other figures to the same scale; 2. ♀ *eurymedon* (Lake Co., Oregon); 3. F₁ ♂ (brood 86.1, ♀ *eurymedon* × ♂ *glaucus*); 4. F₁ ♀ (as in Fig. 3); 5. Backcross ♂ (brood 85.3, black ♀ *glaucus* × ♂ *ex* 85.1); 6. Backcross ♀ (as in Fig. 5); 7. Backcross ♀ (as in Fig. 5); 8. 2nd backcross ♂ (brood 86.9, yellow ♀ *ex* 85.3 × ♂ *glaucus*); 9. 2nd backcross ♀ (as in Fig. 8); 10. 2nd backcross ♀ (as in Fig. 8); 11. ♂ *glaucus* (Montgomery Co., Virginia); 12. ♀ *glaucus* (reared, Montgomery/Giles Co., Virginia); 13. ♀ *glaucus* (Montgomery Co., Virginia); 14. ♀ *glaucus* (Giles Co., Virginia, 1970).

Fig. 8). Fig. 15 shows that the variation in the forewing black margin ratio is inherited in hybrids and backcrosses as a quantitative trait with little evidence of dominance.

Discussion

Brood 86.1, and backcross and F_2 broods 86.7, 86.9, 86.11 and 86.12, show that the cross *eurymedon* ♀ x *glaucus* ♂ can be completely compatible, to the extent that fertile males and females are produced. All pupae of brood 86.1 eclosed 12-13 days after pupation, the normal minimum time for imaginal development. Taken with Clarke and Sheppard's results (1957) and brood 85.1, in all of which only male hybrids eclosed, brood 86.1 suggests that there is variation in the crossability of the two species and that Haldane's Rule need not apply (Haldane, 1922). Thus one of the reasons that Brower (1959) judged *P. glaucus* more closely related to *P. rutulus* than to *P. eurymedon* is sometimes removed. More crosses will be needed to assess the variation in cross-compatibility among these three species.

The ground color of yellow female *P. glaucus* is often just like that of males, and the genes responsible for it should therefore be autosomal (or X-linked), being found in both sexes. The black pigment, which Clarke and Clarke (1983) believe is "added" in black females, is of course Y-linked in its inheritance (Clarke and Sheppard, 1962; Clark and Clarke, 1983). The female hybrids in brood 86.1 support the view that yellow is autosomal or X-linked, because they are nearly as yellow as *P. glaucus* but are carrying a Y chromosome from *P. eurymedon*. The blue scaling of *P. glaucus* females appears also to be autosomal (or X-linked) since, although *P. glaucus* males usually lack the blue, and *P. eurymedon* has reduced blue scaling, the female hybrids have nearly full expression as in *P. glaucus*. The male parent evidently carried the genes, but they were expressed only in females.

The two yellow daughters in 85.3 (Fig. 7) were a surprise, since all the daughters should be carrying the mother's Y chromosome, and there is ample evidence that black is Y-determined (Clarke and Sheppard, 1962). This suggests that *P. eurymedon* has a suppressor of that black phenotype, as discussed below in *P. g. canadensis* (Scriber et al., 1986) and *P. rutulus* (Clarke et al., 1976). The possibility of a suppressor was tested by a further back cross of one of the yellow daughters in brood 85.3 to a male *P. glaucus* (brood 86.9). Black reappeared in six of the seven female offspring (not different from a 1:1 ratio) and this could have been because the yellow female parent was heterozygous for the suppressor. The suppressor cannot be X-linked, because the mother in 86.9 passed it to her yellow daughters but would have passed an X only to her sons. It also cannot be Y-linked, because an F_1 male passed it to some of his daughters (brood 85.3). There are therefore good grounds for invoking an autosomal suppressor of black in *eurymedon*, though another remote

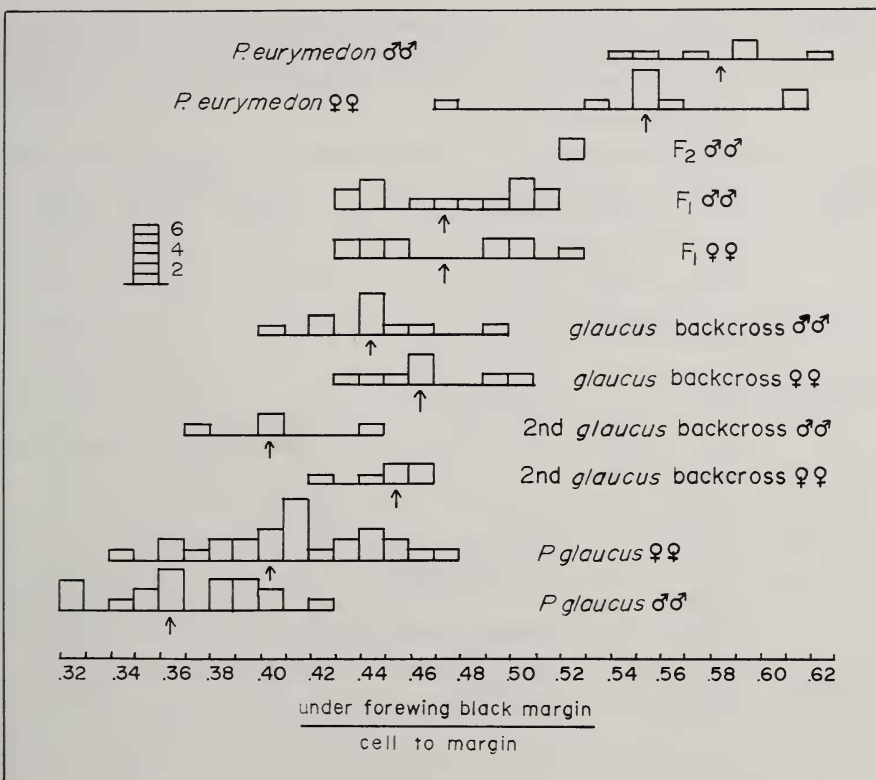


Fig. 15. Distributions of the relative width of the forewing black margin of *P. glaucus*, *P. eurymedon* and hybrids between them. Relative width is given as the ratio of black margin to the distance from cell to margin, measured along vein Cu_1 . Means are marked by arrows.

possibility must be mentioned. The suppressor could have been introduced from *glaucus* of Wisconsin stock by the male parent of the original cross 85.1, but arguing against this are the facts that the Wisconsin male came from south of the range of *P. g. canadensis* and had a black mother and, more importantly, that among the black *glaucus* broods raised in Blacksburg from that particular stock there were none with suppression of the black phenotype.

Section II: Suppression of Black in Hybrids Between *P. g. glaucus* and *P. rutulus*, *P. g. canadensis*, and *P. multicaudatus* (C.A.C.)

There are hybrid zones where naturally occurring crosses can take place between some of these species (see map in Scriber et al. 1986) and all are easy to initiate using the hand-pairing technique.

Hybrids between *P. g. glaucus* and *P. rutulus* (Table 3)

In 1955 we hand-paired a female *rutulus* with a male *glaucus* and obtained 10 males and 8 yellow females (Clarke and Sheppard, 1955),

Table 3. Crosses between black *glaucus* females and *rutulus* males where suppression might occur. Some of the black insects had yellow "brackets" on the forewings, but these are probably normal variants.

Type of Cross	Brood No.	Parent		Offspring			
		Mother	Father	♂♂	Black ♀♀	Interm. ♀♀	Yellow ♀♀
F ₁	14013	black	<i>rutulus</i>	18	0	2 [†]	0
"	15416	"	<i>glaucus</i> California <i>rutulus</i> Vernon, B.C.	1	0	0	2
backcross	8455	"	<i>glauc/rut</i> F ₁ hybrid	8	4	0	2
"	9608	"	"	13	6	0	1
"	9699	"	"	8	3	1	0
"	14173	"	"	18	3	4	0
2nd back.	14655	"	14173	25	16	2	0
"	9769	"	ex bl. <i>glauc.</i> ♀ x (<i>glauc/rut</i>) F ₁ ♂	14	8	0	0
"	14639	"	"	16	4	0	0
"	14642	"	similar to 9769 and 14639	21	17*	1	0
3rd back.	14761	"	ex 14639	9	4	1	0
"	14763	"	"	17	21	0	0

* 6 with yellow showing through papery wings, 11 normal black.

† Ecdysterone treated.

and in the same year found a similar situation (unpublished) when the mother was yellow *glaucus* and the male *rutulus*. However, importantly, the F₁ cross between a black female *glaucus* x *rutulus* male, brood 14013, only yielded females when ecdysterone was injected into the pupae. Then females intermediate in color (and resembling those in brood 85.3, above) were produced. This suggested that here *rutulus* carried a gene which partially suppressed the black pigment (Clarke et al., 1976, Clarke and Willig, 1977, Clarke and Clarke, 1983). Later, in our brood 15416, (previously unpublished) a black *glaucus* female mated to a male *rutulus* from Vernon B.C., Canada, produced one male and two yellow females, suppression of the black here being complete. There was also evidence of suppression on back crossing some male *glaucus/rutulus* F₁ hybrids to black *glaucus* females, since we occasionally obtained broods where the female offspring segregated for black and yellow wing color. On the whole, however, yellow was less evident in the backcross (Table 3).

More difficult to assess from the point of view of the suppressor are minor degrees of yellow in black females. Sometimes the yellow shows through and sometimes there are yellow "brackets" (see Clarke and Clarke, 1983, Figs. 8 and 10). These might be due to partial suppression

or be normal variants of the form, particularly as there is some evidence that the black pigment is laid down late in development (Clarke and Willig, 1977).

Hybrids between *P. g. glaucus* and *P. g. canadensis* (Table 4–8)

The ranges of these two subspecies overlap, and *canadensis* also has common ground with *P. eurymedon* and *P. rutulus*. All these three butterflies are monomorphic, none having a black form, and it would not be surprising if black in *P. g. glaucus* were suppressed in the northernmost part of its range, where *canadensis* will have naturally hybridized with it. This is what in fact happens, but we are stating the case with hindsight, for it was Mark Scriber and his colleagues who greatly clarified the problem of the five species mentioned in this paper (personal communication 1983, Scriber et al., 1986).

Tables 4,5,6 and 7, taken from Scriber et al. (1986), give the details of families where these fundamental principles obtain. Table 4 shows that black is suppressed in F_1 hybrids between *P. g. glaucus* and *P. g. canadensis*. The suppressor is transmitted by F_1 males in backcrosses to black *glaucus* females, since both yellow and black daughters appear (Table 5), but not by "suppressed" yellow backcross females in crosses with *glaucus* males (Table 6). These results are consistent with Scriber et al.'s (1986) hypothesis that the suppressor is X-linked. We ourselves have two similar examples in Table 8. The first (brood 18288) derives from a black female *glaucus* mated to *canadensis*, and this produced yellow females (cf. Table 4); the second (brood 18344) was bred by using a yellow "suppressed" female 18288 mated to a Georgian male (well south of the *canadensis-glaucus* interface) and demonstrates the re-appearance of black (cf. Table 6).

Thus the matter at first sight seems simple - the suppressor is the result of a single autosomal or X-linked gene dominant in effect, and in the examples given there is clear-cut segregation black/yellow. But there are problems.

In Scriber's F_2 results (Table 7) half of the female offspring should be black, but no black appeared. Furthermore, in the backcross to black (see tables 3 and 8) the ratios are not strictly Mendelian, and in practice both in the field and in the laboratory clear-cut black/yellow are often blurred; all grades from black through intermediates to yellow are encountered. An attempt to explain the genetics of this is made in the general discussion; all we wish to emphasize here is that a suppressor mechanism undoubtedly exists in *P. g. canadensis*.

Hybrids between *P. g. glaucus* and *P. multicaudatus* (see Table 9)

In the F_1 broods using either black or yellow female *glaucus* and hand-mating them to male *multicaudatus* we only obtained male offspring (68 in one brood), but in backcrosses of *glaucus* females to hybrid males females were obtained in 8 broods and the sex ratio was

Table 4. Offspring of crosses between black *P. g. glaucus* females and *P. g. canadensis* males (from Scriber et al., 1986).

Pairing Code	Males	Females		Pupae still in diapause at time information was given
		Yellow	Black	
74	2	1	0	0
73	18	17	0	7
112	4	0	0	5
4	1	3	0	5
39	18	4	0	26
75	49	2	0	54
113	7	0	0	10

Table 5. Offspring of crosses between black *P. g. glaucus* females and F₁ hybrid males, *P. g. canadensis* ♀ x *P. g. glaucus* ♂ (from Scriber et al., 1986).

Pairing Code	Male	Female	
		Yellow	Black
6	8	1	3
14	7	5	4
15	40	11	20

Table 6. Offspring of crosses between various *P. g. glaucus* males and yellow females from the backcross of F₁ (*glaucus* x *canadensis*) ♂ x black *glaucus* ♀ (from Scriber et al., 1986).

Pairing Code	Male	Females	
		Yellow	Black
148	2	0	2
154	1	0	7
157	2	0	7
225	4	0	1
155	3	0	1

not significantly upset. Seven of these broods were to yellow *glaucus* females and therefore not informative as regards suppression, but in the single backcross to black which produced butterflies (brood 6329, table 9) the offspring were two males and two yellow females, one of them

Table 7. Offspring of crosses between yellow F₁ females (cross 73, Table 4) and F₁ males (*ex* black *glaucus* ♀ x *canadensis* ♂) (from Scriber et al., 1986).

Pairing Code	Male	Females	
		Yellow	Black
272	29	28	0
288	19	12	0
279	11	6	0

Table 8. Hybrids between *P. glaucus* and *P. g. canadensis* bred from Scriber stock by CAC in England.

Brood No.	Parents		Males	Offspring	
	Mother	Father		Black Females	Yellow Females
18288	Black Wisconsin	<i>canadensis</i>	3	0	3
18344	Yellow 18288	<i>glaucus</i> (Georgia)	8	8	0

Table 9. Hybrids between *P. glaucus* and *P. multicaudatus* (CAC)

Brood No.	Parents		Males	Offspring	
	Mother	Father		Black Females	Yellow Females
6139	black <i>glaucus</i>	<i>multicaudatus</i>	68	0	0
6329	black <i>glaucus</i>	6139	2	0	2

described as "dark yellow." Unfortunately these insects are lost, but there is no reason to doubt the record, particularly in the light of later developments with *rutulus*, *eurymedon* and *canadensis*.

More work is obviously indicated and we have pupae of both species (June 1987).

General Discussion

The purpose of this paper has been to bring together the evidence showing that in four monomorphic yellow Tiger Swallowtails there are suppressors which can inhibit the expression of the black form of *Papilio glaucus*. In *P. eurymedon* the suppressor is clearly autosomal, since it can be transmitted from a father or a mother to a daughter, but the critical evidence is lacking for the other species. If the suppressor in *P. g. canadensis* were also autosomal, the expected frequency of "suppressed" yellow daughters in the F_2 broods of Scriber et al. (1986, Table 7) would be $3/4$ (rather than $1/2$, as from the hypothesis of X-linkage), but the lack of black daughters in those broods is still significant. In all other broods the expectations are the same for both modes of inheritance. Why these suppressors are present is not known. If *P. g. canadensis* and the three western species are derivatives of *P. glaucus* populations with female yellow/black dimorphism, then the suppressors may have been part of the genetic system that cut them off from the ancestral species. Otherwise the existence of suppressors in populations far from the nearest overlap with *P. g. glaucus* (e.g., *P. eurymedon* in central California) is difficult to explain. On the other hand, the history of speciation in the *glaucus* group, perhaps excepting *P. g. canadensis*, is unknown.

Although it was thought possible (Clarke et al., 1976) to associate the presence of the nuclear heteropyknotic body only with the genetic factor for black, and therefore to be able to determine if the western "suppressed" species still carry that factor, it now appears that the heteropyknotic body is not a sure marker for black (Cross & Gill, 1979).

Suppression is common in Batesian mimetic butterflies, many species of which have mimetic patterns limited to females, although inheritance is autosomal. The mechanism of suppression of sex-limited traits is not known, but it appears to exist even in monomorphic species, since male hybrids do not show the mimetic patterns (Clarke and Sheppard, 1972). Crosses with non-mimetic species, however, usually produce more or less intermediate females, with little evidence of interspecific suppression (see *P. fuscus* x *P. polytes*, Clarke and Sheppard, 1972, Plate 42h).

The intermediate forms and unusual Mendelian ratios mentioned earlier would formerly have been explained by differences in expressivity of the gene or genes, but recent studies of the human X chromosome using the techniques of molecular biology suggest other possibilities. For example, an inherited form of mental deficiency appears to be transmitted as an X-linked recessive. The lesion responsible is an X chromosomal abnormality known as the fragile site, which can be induced in cell cultures by various procedures or chemicals. However, as with suppressors, problems soon arose. Occasional males with the fragile X were mentally normal, and some carrier females were affected. Pembrey

et al. (1985) erected a two-stage hypothesis by which the fragile X occurred as a mutant in the male X chromosome but produced no ill effect. However, at the formation of gametes in the daughter of such a male, recombination took place such that the fragile X mutation became more damaging, with half of the daughter's sons being handicapped and half her female offspring carriers. Of particular relevance to race crosses in butterflies are hybrid studies with the fragile X chromosome (Ledbetter et al., 1986). There the threshold for initiation of fragility by various chemicals (for example caffeine) is much reduced if the human X is isolated in a rodent genetic background. It seems not unlikely that everyone has a fragile-X site if the chromosome is suitably manipulated. Possibly the non-suppression of black pigment in *P. g. glaucus* is similarly the exceptional state in the *glaucus* group, with the other species carrying the potential for black permanently suppressed. That possibility could be tested with molecular techniques which have the potential of probing for suppressors in both humans and butterflies.

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